UNITED STATES DEPARTMENT OF AGRICULTURE
BULLETIN No. 869

Contribution from the Bureau of Plant Industry
WM. A. TAYLOR, Chief

THE INHERITANCE OF THE LENGTH OF INTERNODE IN THE RACHIS OF THE BARLEY SPIKE

By

H. K. HAYES, Head of Section of Plant Breeding, Division of Agronomy and Farm Management, College of Agriculture, University of Minnesota, and HARRY V. HARLAN, Agronomist in Charge of Barley Investigations, Office of Cereal Investigations

CONTENTS

WASHINGTON
GOVERNMENT PRINTING OFFICE
1920

UNITED STATES DEPARTMENT OF AGRICULTURE

BULLETIN No. 869

Contribution from the Bureau of Plant Industry
WM. A. TAYLOR, Chief

THE INHERITANCE OF THE LENGTH OF INTER-NODE IN THE RACHIS OF THE BARLEY SPIKE.

By H. K. HAYES, *Head of Section of Plant Breeding, Division of Agronomy and Farm Management, College of Agriculture, University of Minnesota,* and HARRY V. HAR-LAN, *Agronomist in Charge of Barley Investigations, Office of Cereal Investigations.*

CONTENTS.

SCOPE OF THE EXPERIMENTS.

In 1915 a series of studies on the inheritance of the length of internode in the rachis of the barley spike was begun in cooperation with the Minnesota Agricultural Experiment Station. Internode length is a particularly favorable character for such investigations, as a large number of varieties furnish many gradations in internode length and in a pure line the average internode length of the rachis varies comparatively little from year to year.

The project was undertaken for two main reasons, (1) as a study of inheritance in an unusually favorable size character and (2) as a contribution to the question of the taxonomic value of the length of internode of the rachis.

HISTORICAL REVIEW.

The length of internode is frequently referred to as density, and both terms are used in this bulletin. As far back as Linnæus, species were differentiated by this character. With fertility, it has been, consciously or unconsciously, one of the main bases of classification

of most of the modern taxonomists as well. The groups of Schuebler (22)[1], Seringe (23), Heuzé (11, 12), Voss (25), Koernicke (13, 14, 15, 16, 17), Atterberg (2, 3, 4), and Beaven (5) involved variations in density. In 1918 Harlan (10) offered an arrangement which eliminated the question of density from the major groups. It was retained as a minor distinction only, because of the volume of the literature in which it had been used. Its complete elimination would have left too little connection between the author's scheme and the previous usage.

In classifying barleys, density is an obvious and attractive character. When confined to type forms the separations are ideal, but, as with many things in taxonomy, its perfection depends on limited material. The more material that is assembled the more the subdivisions of density have to be increased. Linnæus (18) used the name *Hordeum distichon* to designate the lax 2-rowed and *H. zeocriton* to designate the very dense 2-rowed forms. Schuebler divided *H. distichon* into *erectum* and *nutans*. Eriksson (8) used *genuinum* and *patens* to designate lax and dense subdivisions of *erectum*. Linnæus recognized *hexastichum* and *vulgare* as the dense and lax groups of 6-rowed barleys. Koernicke divided *hexastichum* into *pyramidatum* and *parallelum* and recognized *brachyurum* and *macroterium* of Alefeld (1) as dense and lax subdivisions of *pyramidatum*. The finer the groups were made, the more confusing became the distinctions. The confusion indicated that, while there might be some genetic distinctions, from a taxonomic standpoint there was no clear separation.

In the mode of inheritance the situation is also complicated. As a size character, the accounts are quite favorable as to its constancy, and some varieties are traceable for centuries by this character alone. In recent times Blaringhem (7), possibly following the lead of the Svalof station, made quite elaborate studies of barley density in France. Harlan (9) found density to be quite a stable character. Regarding the mode of inheritance, the studies, however, are largely unsatisfactory. The taxonomic papers contain no comprehensive measurement of density. Many of the inheritance papers are equally inadequate. In many instances fertility and density are treated together, as by Von Tschermak (24). Density has been regarded as recessive by Blaringhem (7) and as dominant by Von Tschermak.

The only paper which is directly concerned with the method of study used in this article is that of Biffen (6), who obtained results closely parallel to those presented herein. In three crosses to which he paid particular attention, Biffen found the F_1 generation to be slightly more dense than the lax parent, although the numbers of individuals in F_1 were small. The F_2 generation consisted in each case of plants

---

[1] The serial numbers in parentheses refer to "Literature cited," at the end of this bulletin.

with spikes as lax or as dense as those of the parents, with a series lying between these extremes which could not be satisfactorily classified without further test. In some crosses the F_2 generation curves plotted from the measurements showed two peaks and in others three. In a cross of *zeocriton × nutans* groups of plants were centered about internode lengths of 2.2 and 3 millimeters, respectively. The 65 plants constituting the more dense group were tested in the F_3 generation by seeding all individuals with internode lengths ranging from 1.8 to 2.6 millimeters. Of these 65 plants, 55 proved homozygous and 10 were heterozygous. Thus, 55 out of a total of 209 plants grown in F_2 bred true for densities near that of the dense parent, or a close approximation of a 1:3 ratio. No genetic analysis is given of crosses which appear to have three groups in F_2, or lax, dense, and intermediate forms.

Study has been made of the inheritance of density in wheat and, although apparently pertinent, it is not comparable to one made in barley, for the reason that the dense wheats are clubbed at the tip and thus introduce a condition which makes comparison difficult. Gradations were found in F_2 between the parents. Nilsson-Ehle (20) explained these on the basis of two kinds of factors, a positive factor for compactness which partially inhibited the action of one or more lengthening factors. Parker (21), in a more extensive study in which the statistical method was used, concludes that numbers such as Nilsson-Ehle used were inadequate to demonstrate his hypothesis. In Parker's studies segregation occurred in F_2, but it seemed impossible to determine the number of factors involved.

PURE-LINE VARIETIES USED IN THESE STUDIES.

With the exception of the Jet variety, the pure lines used in crosses in the studies here reported are quite typical representatives of the three degrees of density much used by taxonomists in the 6-rowed barley. Their relationships are most easily made apparent by use of the taxonomic key which follows. The variations in density are well shown in Plate I.

KEY TO BARLEY VARIETIES USED IN DENSITY STUDIES.

Hordeum vulgare pallidum (6-rowed, hulled, awned, white).
    Subvariety *typica*, spike lax, pure-line Manchuria.
    Subvariety *parallelum*, spike dense, pure-line Reid Triumph.
    Subvariety *pyramidatum*, spike very dense, pure-line Pyramidatum.
Hordeum distichon palmella (2-rowed, hulled, awned).
    Subvariety *nutans*, spike lax, pure lines Hanna and Steigum.
    Subvariety *erectum*, spike dense, pure-line Svanhals.
    Subvariety *zeocriton*, spike very dense, pure-line Zeocriton.

Jet is a naked, black, 2-rowed barley of about the same spike density as Steigum. Although Hanna and Steigum belong to the same group, Steigum is slightly more dense than Hanna. *Deficiens*

was not used in any of the crosses, but is included because of an inherited variation found in it. The form used is lax and differs from *nutans* in having only rudiments of lateral florets.

RELIABILITY OF EXPERIMENTAL METHODS.

In this investigation the feasibility and accuracy of density determinations were tested in many ways. The length of internode was computed from the measurement of 10 internodes in the middle of the spike. All measurements were taken in millimeters.

To test the observational accuracy, the populations from which the density of three parents was determined were remeasured after a lapse of three weeks. The difference in the measurements of Manchuria was 0.02 ± 0.01 mm.; of Zeocriton, 0.04 ± 0.01 mm.; and of Hanna, 0.12 ± 0.02 mm. Differences as small as 0.2 mm. in means of varieties, therefore, can not be demonstrated by the method used. As seasonal fluctuations in the means often are as great as this, the method of taking the data is sufficiently accurate.

The internode measurement was taken in the middle of the spike, not only because of the greater convenience, but because experiments indicated that the internodes in this zone are less variable than in other parts of the spike. Measurements were taken in different parts of the spike on approximately 100 plants of each of the Zeocriton, Pyramidatum, Manchuria, and Hanna parents. Where the spikes were long enough, six different sections were measured, i. e., nodes 1–11, 3–13, 5–15, 7–17, 11–21, and the last 10 internodes toward the tip. In Pyramidatum the measurements for nodes 7–18 and 11–22 could not be made. The means for these measurements, in millimeters, were as follows: Zeocriton, 1.37, 1.47, 1.66, 1.81, 1.95, and 2.15; Pyramidatum, 1.98, 2.12, 2.17, and 2.15; Manchuria, 2.88, 3.13, 3.35, 3.42, 3.36, and 3.38; Hanna, 3.90, 4.17, 4.40, 4.47, 4.35, and 3.90.

The Zeocriton is the only variety in which there is a progressive increase in internode length from the base to the tip. If the factor or factors determining this progressive increase segregate in a normal way, the progeny of a cross between this type and one in which this peculiarity is absent or less pronounced, as in Pyramidatum, might contain types easily misinterpreted. The mean of a pure recessive for a main density factor might easily differ by 0.2 to 0.4 mm. from the parent, due to the gain or loss of this marked progressive increase of internode length found in Zeocriton.

Contrary to results previously reported by Harlan (9), no change in internode length due to the presence of sterile nodes was observed.

PLATE I.

AVERAGE HEADS OF THE PARENTAL VARIETIES USED IN THE DENSITY STUDIES.

Left to right: No. 333, Deficiens; 1039, Zeocriton; 458, Svanhals; 17, Steigum; 454, Hanna; 460 Jet; 476, Pyramidatum; 404, Reid Triumph; 360, Manchuria.
(Photographed by Horton.)

PLATE II.
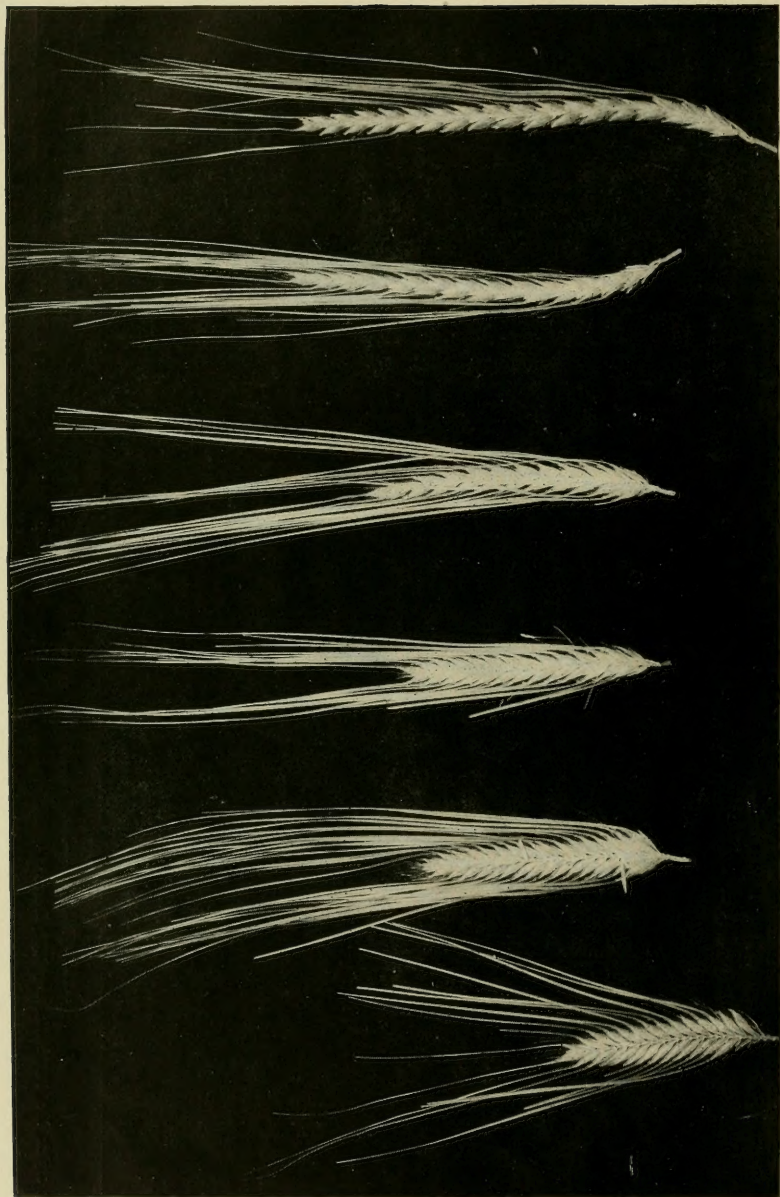
AVERAGE HEADS OF THE ZEOCRITON (LEFT), HANNA (RIGHT), AND FOUR HOMOZYGOUS F₃ AND F₄ LINES.

The mean densities are as follows: Zeocriton, 1.9; Hanna × Zeocriton 448–1, 2.3; 448–5, 2.9; 448–11–3, 3.7; 448–16, 4.3; Hanna, 4.6. All means as given are from 1918 results. (Photographed by Horton.)

EFFECTS OF ENVIRONMENT AND VARYING SOURCES OF SEED ON DENSITY.

Wide differences of condition, such as obtain in California as compared with Minnesota, are sufficient to modify the expression of density. As will be seen by referring to Table I, the annual fluctuations of density measurements in a pure variety are not sufficient in Minnesota to introduce any large error in the conclusions, especially when it is considered that progeny are compared only with parents of the same year's growth.

In 1918 there was an opportunity to test the effect of vigor of plant on density. One section of the nursery produced Manchuria plants which averaged 110 centimeters in height, while the same strain in another part of the nursery averaged only 82 centimeters. A similar difference was apparent in Svanhals. The internode lengths of the Manchuria plants were 3.36 ± 0.01 and 3.33 ± 0.01 mm., respectively, and of Svanhals, 2.56 ± 0.01 and 2.65 ± 0.01 mm., respectively, both being within the limits of observational accuracy.

Sometimes the F_1 generation of a cross was grown in the Washington greenhouse and the seed from it was still rather immature when sown in Minnesota. Plants of Manchuria from greenhouse seed gave a mean internode length of 3.22 ± 0.02 mm., as compared with 3.34 ± 0.02 mm. in plants from field-grown seed. In Svanhals, the difference was less, 2.49 ± 0.02 as compared with 2.52 ± 0.01 mm. Neither variation is large enough to have any particular significance in this study.

PURITY OF PARENTAL FORMS.

The variation which may be expected in a pure line within a single season and from season to season is shown in Table I. The 6-rowed varieties gave about the same mean average length of internode in all three seasons. With the 2-rowed varieties there was more seasonal fluctuation in average density. All varieties of this group gave a higher mean length of internode in 1918 than in 1917. In Steigum the seasonal difference reached its maximum of 0.51 ± 0.03 mm., and in Hanna the seasonal variation also was large. Individuals of different densities in the different varieties were selected as parents. The only possibility of inherited variation within the same variety occurred in *deficiens*. The progeny of plant 333–5–1 is significantly lower in mean density. Only two or three *deficiens* types have been grown in the nursery, and the progeny showed no evidence of hybridization. As the chance of mixture or accidental crossing is small, it might be interpreted that we had chanced to select a spike in which a sudden change in the factors for density had taken place.

TABLE I.—*Record of spike density in pure-line barley parents and in their progeny.*

Variety	Generation	Year	Density	1.6	1.8	2.0	2.2	2.4	2.6	2.8	3.0	3.2	3.4	3.6	3.8	4.0	4.2	4.4	4.6	4.8	5.0	5.2	5.4	5.6	Total	Mean	Standard deviation	Coefficient of variability
Zeocriton:																											
1039	P_1	1917	1.8	4	16	8		1																	24	*mm.* 1.87±0.01	0.09±0.01	4.81±0.47
1039–1	P_2	1918	1.9	1	34	53	16																		107	1.95±.01	.15±.01	7.69±.35
1039–2	P_2	1918	1.9		19	29	6	1																	56	1.95±.01	.15±.01	7.69±.49
Svanhals:																											
45s	P_1	1916	2.5					6	56	31	8														101	2.68±.01	.14±.01	5.22±.25
45s–1	P_2	1917	2.6					6	10																16	2.53±.02	.10±.01	3.95±.47
45s–2	P_2	1917	2.7					7	8																15	2.51±.02	.10±.01	3.98±.49
45s–3	P_2	1917	2.9					4	12	2															18	2.58±.02	.11±.01	4.26±.48
45s–4	P_2	1917	3.0					7	5																12	2.48±.02	.12±.01	4.03±.55
45s–5	P_2	1917	2.6					9	9																16	2.54±.02	.12±.01	4.72±.56
45s–2–1	P_3	1918	2.6					8	29	43	11	1													93	2.73±.01	.18±.01	6.59±.33
45s–2–2	P_3	1918	2.7					6	42	46	13	1													109	2.72±.01	.17±.01	6.25±.29
45s–3–1	P_3	1918	2.8					7	50	35	15														107	2.71±.01	.16±.01	5.90±.27
45s–3–2	P_3	1918	2.7					10	42	43	9														105	2.70±.01	.16±.01	5.93±.28
Steigum:																											
17	P_1	1916	3.2									10	22	18	4	1									55	3.47±.02	.18±.01	5.19±.33
17–2	P_2	1917	3.2										2	13	6										21	3.64±.02	.12±.01	5.30±.34
17–3	P_2	1917	3.2									2	2	8	3	1									16	3.59±.03	.20±.02	5.57±.66
17–4	P_2	1917	3.5									1	1	5	6	1									14	3.73±.02	.16±.02	4.29±.55
17–5	P_2	1917	3.5										1	5	7	2	4								19	3.62±.03	.20±.02	5.52±.60
17–7	P_2	1917	3.7										2	8	7	2	1								20	3.71±.03	.17±.02	4.58±.49
17–9	P_2	1917	3.8										1	5	9	2									17	3.75±.03	.18±.02	4.80±.56
17–10	P_2	1917	4.0											7	7										19	3.72±.02	.13±.01	3.49±.38
17–12	P_2	1917	4.1										3	8	3										15	3.65±.03	.19±.02	5.21±.64
17–13	P_2	1917	4.1										2	13	4			3							18	3.69±.02	.18±.02	4.88±.55
17–14	P_2	1917	4.4										4												22	3.62±.02	.15±.01	4.14±.42
17–5–1	P_3	1918	4.5										1	1	9	21	12	4							47	4.04±.02	.18±.01	4.46±.31
17–5–2	P_3	1918	4.4										1	1	16	25	4	1	2						47	3.95±.01	.13±.01	4.80±.26
17–7–1	P_3	1918	4.5										2	2	23	15	8	1	1						51	3.95±.02	.20±.01	5.06±.34
17–9–2	P_3	1918	3.9										5	5	35	24	5	4	1						78	3.95±.02	.23±.01	5.82±.31
17–10–1 and 2	P_3	1918	3.9										2	7	17	20	6	4							63	4.02±.02	.20±.01	4.98±.30
17–12–1	P_3	1918	3.9									1	2	10	9	6	5								40	3.99±.02	.19±.02	4.76±.36
17–13–1	P_3	1918	3.3										1	19	14	28	2	3							69	4.01±.02	.22±.02	4.49±.32
17–14–1	P_3	1918	4.2										1	14	11	7	4								28	3.93±.03	.22±.02	5.60±.50
	P_3	1918	3.4											11		12									28	3.94±.02	.15±.01	3.81±.34
Jet:																											
454	P_1	1916	3.4										11	25	20	9	5	3							73	3.75±.02	.26±.01	6.93±.39
454–1	P_2	1917	3.7										1	5	7	1	1								14	3.77±.03	.17±.02	4.51±.57
454–2	P_2	1917	3.9										1	7	6										14	3.67±.02	.12±.02	3.27±.42
454–3	P_2	1917	4.0										3	7	2	1									13	3.62±.03	.17±.02	4.60±.61
454–4	P_2	1917	4.3											9	3										12	3.65±.02	.09±.01	2.47±.34

A large statistical data table (rotated) giving inheritance measurements for the barley spike across varieties. Leftmost columns list the strain/row designation, generation, and year; the remaining columns give frequency distributions and computed means with probable errors.

Strain	Gen.	Year																							Mean ± P.E.		
454-5	P₂	1917											1	7	2	7	1							4.5	11	3.66±.03	4.10±.59
454-1-1	P₃	1918										2	1	7	31	6	1							4.1	50	3.86±.02	4.66±.31
454-1-3	P₃	1918									1	1	22	22	7									3.8	59	3.89±.02	4.63±.29
454-3-1	P₃	1918										7	32	28	1									3.8	67	3.94±.01	4.31±.25
454-3-2	P₃	1918									7	29	25	4										3.5	71	3.96±.02	5.05±.29
Hanna:																											

TABLE I.—*Record of spike density in pure-line barley parents and in their progeny—Continued.*

Variety.	Generation.	Year.	Density.	Class centers of density for progeny (millimeters).																					Total.	Mean.	Standard deviation.	Coefficient of variability.
				1.6	1.8	2.0	2.2	2.4	2.6	2.8	3.0	3.2	3.4	3.6	3.8	4.0	4.2	4.4	4.6	4.8	5.0	5.2	5.4	5.6		*mm.*		
Manchuria—Contd.																												
560-3-1	P₃	1918	3.5									16	45	16	2	2									81	3.43±.01	.17±.01	4.95±.26
560-3-2	P₃	1918	3.3									13	31	22	7	1	1								75	3.48±.02	.20±.01	5.75±.32
560-5-1	P₃	1918	3.2									5	27	8	3		3	1							52	3.56±.03	.29±.02	8.15±.54
560-5-2	P₃	1918	3.1								1	18	27	9	6	5									61	3.43±.02	.19±.01	5.54±.34
Deficiens:																												
333	P₁	1916	4.0												8	22	29	17	13	8	1				98	4.27±.02	.29±.01	6.79±.33
333-2	P₂	1917	5.0											1	2	5	5	1	1			1	1		17	4.07±.04	.23±.03	5.65±.65
333-5	P₂	1917	4.5											2	2	2	1	1	3	3					14	4.00±.05	.26±.03	6.50±.83
333-2-1	P₃	1918	4.0														7	3	3						13	4.34±.03	.16±.02	3.69±.49
333-2-2	P₃	1918	4.5														6	8	11	3					22	4.51±.05	.32±.03	7.10±.72
333-2-3	P₃	1918	3.7													8	12	15		2					48	4.35±.02	.32±.02	7.06±.39
333-5-1	P₃	1918	3.6									1	1	14	15	13	6								50	3.82±.02	.22±.01	5.76±.35
333-5-2	P₃	1918	4.4										1		1		2	1	4				1		9	4.49±.09	.41±.07	9.13±1.45

INHERITANCE OF LENGTH OF INTERNODES IN CROSSES BETWEEN PURE LINES.

Each cross studied has been considered as a separate family. For convenience, the data from each such family will be discussed separately. In considering crosses, statements will be made as to the number of homozygous and heterozygous forms. Such statements can be only relative. Using the variability of the pure lines as a standard, it is assumed that progeny lines of low variability are homozygous, while those of high variability are heterozygous. There is no reasonable doubt of the classification of the extremes, but there is a borderland where the most varying homozygotes may be in doubt.

FAMILY MANCHURIA (360) × SVANHALS (458).

The actual F_1 generation of the cross between Manchuria and Svanhals, which was the basis of later generations discussed in this bulletin, was grown in 1915. A considerable number of crosses between these same pure lines of Manchuria and Svanhals were made in 1917 in the greenhouse at Washington, D. C. The data for the F_1 reported in Table II (sec. A) are from this greenhouse seed. On the basis of the coefficient of variability, this F_1 generation proved no more variable than the parents.

In 1917 the mean average density in millimeters of the Svanhals parent was 2.53 ± 0.01 mm.; of the Manchuria, 3.34 ± 0.01 mm.; and of the F_1, 2.70 ± 0.01 mm. There is almost a complete dominance of the dense over the lax form.

An F_2 generation was grown both in 1916 and in 1918. The means for these two F_2 generations were 2.94 ± 0.01 and 2.96 ± 0.02 mm., respectively. The variation as determined by the frequency distribution and the coefficient of variability was much greater in F_2 than in F_1 or in the parental forms, the coefficient of variability of the F_1 generation being 6.30 ± 0.30 mm. and of the F_2 generations of 1916 and 1918, 10.20 ± 0.27 and 11.82 ± 0.48 mm., respectively.

Thirty-two F_3 lines, representing all F_2 types of density, were grown. Thirteen of these F_2 plants appeared to give homozygous progeny in the F_3 generation. The writers recognize that too few plants were grown in F_3 to determine with certainty which forms were homozygous. Eight of these 13 lines were continued in F_4, and five of these appeared to be homozygous. These results show that a considerable number of the F_2 plants selected bred true in F_3, although no conclusion as to the actual percentage can be made.

The five types which proved to be homozygous in F_4 gave mean densities as follows: 378–1, mean 2.57 ± 0.01 mm.; 378–11, mean 2.64 ± 0.01 mm.; 378–14, mean 3.37 ± 0.02 mm.; 378–23, mean 2.55 ± 0.01 mm.; 378–31, mean 2.58 ± 0.01 mm. Selection 378–88 gave the highest coefficient of any third-generation line. Two heads were selected which bred true in F_4 for densities near the Manchuria parent.

TABLE II.—*Record of spike density in parent pure lines of barley varieties and in successive generations of their progeny.*

Variety.	Generation.	Year.	Density.	Class centers of density for progeny (millimeters).																			Total.	Mean.	Standard deviation.	Coefficient of variability.
				1.6	1.8	2.0	2.2	2.4	2.6	2.8	3.0	3.2	3.4	3.6	3.8	4.0	4.2	4.4	4.6	4.8	5.0	5.2	5.4	5.6				
SEC. A.—Manchuria (360)×Svanhals (458)=378:																											
Manchuria 360	P₁	1916	3.2 to 4.4					6	56		4	11	57	27	8			1							104	3.47±0.01	0.18±0.01	5.19±0.24
Do	P₂	1917	3.1 to 3.5					30	44	31	1	66	97	20											187	3.34±.01	.14±.00	4.19±.15
Do	P₃	1918					2	31	107	8	52	130	55	18	8		4	1							269	3.46±.01	.22±.01	6.36±.18
Svanhals 458	P₁	1916	2.5 to 3.0					7	52	30	48	3													101	2.68±.01	.14±.01	5.22±.25
Do	P₂	1917	2.6 to 2.8			2		9	61	97	8	3													77	2.53±.01	.11±.00	4.33±.24
Do	P₃	1918						6	24	37	84	4													414	2.71±.01	.17±.00	6.27±.15
360 × 458	F₁	1917							11	3	30	17	22	10	4	1	1		1						100	2.70±.01	.17±.01	6.30±.30
378	F₂	1916					2	26	55	1		9	10		3	1									333	2.94±.01	.30±.01	10.20±.27
378	F₃	1918						52	32																138	2.96±.02	.35±.01	11.82±.48
378-1	F₂	1917																							32	2.54±.02	.21±.02	8.27±.70
378-1 (5 plants)	F₃	1918	2.6 to 2.9			1						1													109	2.57±.01	.17±.01	6.61±.30
378-1-6	F₄	1918	2.4 to 3.1					10	25	21		1	7	4											101	2.44±.01	.15±.01	6.15±.29
378-6	F₃	1917	2.5					12	48	16	15	1		11		2	3								72	3.13±.03	.36±.02	11.50±.65
378-8	F₃	1918	3.4					3	13	29	12	3	4	16	3	2									38	3.11±.01	.18±.01	5.79±.45
378-8 (5 plants)	F₄	1918	3.5					11	17	9	13	7	24	1	5	2		2							94	3.26±.01	.30±.01	9.20±.45
378-8-6	F₄	1917	3.1				2	4				1	18	16	1	2		2							98	3.28±.01	.29±.01	8.84±.43
378-9	F₄	1918	3.4							1		7	4	1											11	3.33±.04	.25±.04	7.51±1.08
378-11	F₃	1917	2.8						25	12	5	29	6												49	2.62±.01	.15±.01	5.73±.39
378-11 (5 plants)	F₄	1918	2.5 to 3.0					12	48	16	5	31	9												82	2.64±.01	.16±.01	6.06±.32
37X-11-6	F₄	1918	2.9					3	43	29	4	33	35				7								80	2.69±.01	.14±.01	5.20±.28
378-12	F₃	1917	2.9					11	17	19	8	30	23		5										51	2.71±.02	.29±.02	10.70±.71
378-13	F₃	1917	3.1				2	4	12	21	3	21	11	1			1								60	2.84±.02	.28±.02	9.86±.61
378-14	F₃	1918	3.3																						55	3.14±.02	.17±.01	5.41±.35
37X-14 (5 plants)	F₄	1918	3.2				3		16		2	2	3												91	3.37±.01	.23±.01	6.82±.34
378-11-6	F₄	1917	3.7																						97	3.36±.01	.20±.01	5.95±.29
378-19	F₃	1917	3.2							3			8												72	3.24±.01	.17±.01	5.25±.30
378-20	F₃	1918	3.1				1		11	2	3		2	1		1									50	3.21±.02	.17±.02	5.30±.36
378-22	F₃	1917	2.7							1	2														58	2.49±.02	.27±.02	10.84±.68
378-23	F₃	1917	2.7			2	11	24	16		4	2													59	2.42±.01	.11±.01	4.55±.28
378-23 (5 plants)	F₄	1918	2.5 to 2.9			1	7	39	13	23	12	1													151	2.55±.01	.15±.01	5.88±.33
378-23-6	F₃	1918	2.5			1	6	61	57	18	21	5													58	2.66±.01	.17±.01	6.39±.35
378-24	F₃	1917	3.0					12	38	16	16	17													54	2.83±.03	.32±.01	11.31±.71
378-25	F₃	1917	2.9					7	11	9	21	5													45	3.03±.03	.27±.03	7.26±.47
378-26	F₃	1917	3.0					2	13	8	13	17		1											50	3.67±.03	.23±.03	7.72±.72
378-27	F₃	1917	3.3					11	15	12	9	16													50	3.03±.02	.23±.02	8.39±.57
378-28	F₃	1917	3.4				1	5	19	9	16	8													53	3.08±.02	.20±.01	6.49±.44
378-29	F₃	1917	3.6				8	6	14	12	16	4													46	3.77±.02	.25±.02	9.03±.59
378-30	F₃	1917	3.4				3	15	11	13	15	6	1												37	2.85±.03	.29±.02	10.18±.72
378-31	F₄	1917	2.4		2			28	20	31	8	7	1												115	2.51±.01	.12±.01	4.79±.38
378-31 (5 plants)	F₃	1918	2.6		2		3	37	43	6	2	6				1									88	2.58±.01	.17±.01	6.75±.34
378-32	F₃	1917	3.0					2	6	6	8		4	1	1										33	2.96±.04	.31±.03	10.47±.87

TABLE II.—*Record of spike density in parent pure lines of barley varieties and in successive generations of their progeny*—Continued.

Variety.	Generation.	Year.	Density.	Class centers of density for progeny (millimeters).																					Total.	Mean.	Standard deviation.	Coefficient of variability.
				1.6	1.8	2.0	2.2	2.4	2.6	2.8	3.0	3.2	3.4	3.6	3.8	4.0	4.2	4.4	4.6	4.8	5.0	5.2	5.4	5.6				
SEC. C.—Pyramidatum (476)×Jet (454)=325:																												
Pyramidatum 476	P₁	1916	2.1 to 2.4			11	20	2																	33	2.15±.01	.11±.01	5.12±.43
Do	P₂	1917	2.1 to 2.5		2	32	89	17																	138	2.18±.01	.12±.01	5.50±.22
Do	P₃	1918			2	97	83	14																	196	2.11±.01	.13±.01	6.16±.21
Jet 454	P₁	1916	3.4 to 4.5										11	25	20	9	5	3							73	3.67±.01	.26±.01	6.93±.39
Do	P₂	1917	3.4 to 4.1										5	35	20	3	1								64	3.75±.02	.15±.01	4.09±.24
Do	P₂	1918											1	18	106	90	22	7	3						247	3.86±.01	.15±.01	4.85±.15
476 × 454	F₁	1918						11	16	51	9														87	2.86±.01	.12±.01	3.11±.16
325	F₂	1916					5	5	19	14	20	8	5	7	2									84	2.92±.04	.48±.02	16.44±.87
325	F₃	1918					8	9	6	25	9	9	8	3	4	11								121	3.10±.03	.57±.04	18.3±.81
325-1	F₃	1917					2	3		3	3	10			1									29	2.74±.05	.42±.05	15.33±1.38
325-2	F₂	1917	3.1 to 3.5			1	2		1	4		17	7	8	1									28	2.89±.05	.38±.05	13.15±1.20
325-2	F₃	1917			1					1	1													18	2.21±.03	.21±.03	9.50±1.07
325-4	F₃	1917									1													34	2.23±.02	.15±.02	6.73±.53
325-5(10 plants)	F₄	1918									1	1	2	6	2	12	2							26	3.15±.02	.18±.02	5.71±.53
325-7	F₃	1917				1				1	1		6	65			1				1			213	3.43±.01	.25±.01	7.29±.24
325-8	F₃	1917	2.9 to 3.5								2		6	2											17	2.80±.05	.11±.05	16.79±1.98
325-9	F₃	1917				1			1	1	1		8	1	1									14	2.92±.07	.49±.06	14.64±1.90
325-10	F₃	1917				1	2		3		1		2	2	1									13	2.88±.08	.46±.06	16.78±2.26
325-11	F₃	1917	3.0 to 3.8				2	2	5	4		2	2	1	1									15	2.63±.08	.45±.06	15.97±2.01
325-12	F₃	1917				1	3	4	1		1													15	2.71±.08	.47±.06	17.11±2.25
325-13(10 plants)	F₄	1918									1		1	33	13									14	3.26±.06	.16±.02	17.34±2.28
325-13	F₃	1917	3.5							1	2	6	49	33	5						1			13			4.91±.65
325-14	F₃	1918	3.8																					119	3.58±.03	.19±.01	5.45±.24
325-15	F₃	1917						1		2	1		6	6	2	2								19	3.06±.11	.21±.02	5.87±.64
325-16(9 plants)	F₄	1918											3	16	6	39	1			5	8			11	3.34±.04	.54±.08	17.65±3.21
325-16-7	F₃	1917	3.0 to 3.5							1			6	34	39	1				1				112	3.74±.11	.19±.03	5.69±.82
325-17	F₃	1918					4	5	6															15	3.04±.01	.22±.11	20.39±2.61
325-18	F₃	1917	2.0 to 2.7			4	8	1	10		1													11	2.33±.04	.62±.01	9.01±1.30
325-18(10plants)	F₄	1918				24	47	22	4															13	2.15±.02	.21±.04	5.12±.68
325-19	F₃	1917	2.7			2	6	3	3															107	2.24±.03	.11±.01	8.93±.41
325-20(10plants)	F₄	1918				1	6	10																15	2.32±.02	.20±.01	8.62±1.06
325-20	F₃	1917	2.1 to 2.5			5	12	30	4	7	1													89	2.31±.04	.20±.02	5.19±.60
325-21	F₃	1917	4.0											5	13	63	16							13	2.47±.04	.12±.01	8.50±.43
325-21(10plants)	F₄	1918	3.5 to 3.9											13	36			8						140	3.57±.03	.21±.03	5.88±.78
325-22	F₃	1917										1			6	6		5						17	3.95±.01	.18±.02	5.57±.22
325-22(10plants)	F₄	1918	3.3 to 3.9					4	34		1	4	16	45	39	24	5							133	3.60±.02 3.72±	.22±.01	5.00±.58 6.91±.24

SEC. D. — Hanna (460) × Reid Triumph (404)=406:																												
Hanna 460	P₁	1916																				83	4.12± .02	31± .02	7.32± .39
Do	P₂	1917																			1	167	4.23± .01	22± .01	5.20± .19
Do	P₃	1918																				209	4.56± .01	26± .01	5.70± .19
Reid Triumph (404)	P₁	1916											16	49	28	4						97	2.64± .01	15± .01	5.68± .27
Do	P₂	1917							2	1	20	30	2	41	53	9	5		1			105	2.73± .01	13± .01	4.76± .22
Do	P₃	1918							36	36	24	3	34	131	112	30	29	21					317	2.69± .01	19± .01	7.06± .19
406	F₁	1916						1		3	50	24	1	4	18	2	2	3	1				131	3.29± .02	33± .02	10.03± .42
406-1	F₃	1917	3.6 to 4.9							7	7		5		3	4	1						16	2.81± .05	21± .03	7.47± .89
406-1 (8 plants)	F₃	1918	4.1 to 4.7					14	6	24	25	21	80	43	29		1	4					181	3.19± .01	18± .01	7.84± .23
406-2	F₃	1917				4	1	1	7	8	2	1	8	1	2								17	2.72± .01	25± .01	6.67± .91
406-3 (10 plants)	F₃	1918	2.7 to 3.0			2	24	23	21	17	1	55	43	24									154	3.37± .03	18± .01	8.82± .85
406-4	F₄	1917	2.7 to 2.9	2	29																		14	2.84± .02	24± .01	4.98± .34
406-4 (10 plants)	F₄	1918	2.5 to 3.0										6	6									172	3.21± .01	16± .01	8.61± .63
406-4-8	F₄	1918	3.0 to 3.5										6	6									20	3.37± .03	29± .03	6.04± .53
406-5	F₃	1917	3.2																				16	2.84± .03	20± .02	6.13± .75
406-5 (10 plants)	F₃	1918	3.2																				19	3.72± .01	17± .01	4.57± .54
406-6	F₄	1917	3.6 to 4.3						10														204	3.93± .01	21± .01	5.34± .58
406-7	F₃	1917	2.4	7	21																		12	4.43± .01	28± .01	6.32± .72
406-7 (9 plants)	F₃	1918	2.5																				14	3.68± .01	46± .09	12.50±1.72
406-8	F₄	1918	2.2 to 2.6																				150	2.43± .01	13± .02	5.35± .68
406-8 (10 plants)	F₃	1918	2.9																				16	2.43± .01	20± .01	8.23± .32
406-9	F₄	1917	3.5 to 4.4																				16	4.01± .04	25± .03	8.23± .74
406-9 (10 plants)	F₃	1918	3.7	7		10																		174	4.32± .01	29± .01	6.71± .24
406-9-1	F₄	1917	4.0																				19	3.74± .01	25± .03	6.68± .73
406-9-10	F₄	1918	3.2																				239	4.20± .01	30± .01	6.98± .73
406-10	F₄	1918	4.2 to 4.4																				21	4.30± .04	31± .04	6.52± .84
406-10 (10 plants)	F₃	1918	4.6																				14	3.64± .01	24± .01	6.80± .36
406-11	F₄	1917	2.9																				14	3.66± .02	39± .02	6.39± .74
406-11 (10 plants)	F₃	1918	2.8 to 3.2		1																		164	4.10± .01	16± .04	7.64± .26
406-12	F₄	1917	3.0																				18	4.32± .02	27± .01	6.04± .59
406-12 (4 plants)	F₄	1918	3.1																				202	2.84± .02	33± .02	8.80± .45
406-14	F₃	1917	3.0 to 3.5																				24	3.23± .04	16± .01	9.73± .78
406-16	F₃	1918	3.5																				87	3.29± .03	32± .03	5.26± .55
406-16 (10 plants)	F₄	1918	3.2																				35	3.23± .02	17± .01	6.98± .25
406-16-4	F₄	1917	2.8 to 3.4																				21	3.36± .02	29± .02	7.14± .62
406-16-7	F₄	1918	3.0 to 3.5																				287	2.97± .01	24± .02	9.40± .76
406-18	F₄	1917	3.4	1																			30	3.40± .01	28± .01	6.06± .50
406-18 (10 plants)	F₃	1918	3.0																				35	3.01± .01	18± .01	6.06± .21
406-18-5	F₄	1918	3.3																				33	2.66± .02	15± .02	5.29± .42
406-18-9	F₄	1918	2.8 to 3.4																				370	2.06± .01	19± .02	5.64± .48
406-19	F₄	1917	3.4																				36	3.29± .02	26± .03	6.21± .58
406-19 (10 plants)	F₃	1918	3.0 to 3.5	1																			31	3.06± .01	40± .01	7.90± .25
406-20	F₄	1917	3.5																				26	3.29± .04	32± .04	12.35±1.09
406-21	F₄	1918	4.0																				235	3.57± .04	25± .03	3.96± .79
406-22	F₃	1917	3.6 to 4.5																				29	4.10± .01	40± .05	6.10± .62
406-22 (10 plants)	F₄	1918	5.0																				29	4.37± .01	25± .01	7.78± .20
406-23	F₃	1917					1																57	3.99± .02	27± .02	6.77± .43

TABLE II.—*Record of spike density in parent pure lines of barley varieties and in successive generations of their progeny*—Continued.

Variety	Generation	Year	Density	Total	Mean	Standard deviation	Coefficient of variability
SEC. F.—Hanna (460)×Zeocriton (1039)=448:							
Hanna 460	P_1	1916	3.6 to 4.9	83	4.12±.02	.31±.02	7.52±.39
Do	P_2	1917	4.1 to 4.7	167	4.43±.01	.22±.01	4.97±.18
Do	P_3	1918		209	4.56±.01	.26±.01	5.70±.19
Do	P_1	1917		34	1.87±.01	.09±.01	4.81±.47
Zeocriton 1039	P_2	1918		153	1.95±.01	.15±.01	7.69±.30
Do	P_1	1916		141	2.99±.04	.69±.03	23.08±.97
448	F_2	1916	2.1	48	2.10±.02	.17±.01	8.10±.56
448-1	F_3	1917	1.9 to 2.4	213	2.30±.01	.17±.01	7.39±.24
448-1 (4 plants)	F_4	1918	2.4	91	2.39±.03	.38±.01	15.89±.81
448-2	F_3	1917	2.4	32	2.39±.07	.57±.05	23.85±2.11
448-3	F_3	1917	2.3	60	2.40±.03	.32±.02	13.33±.83
448-4	F_3	1917	2.4	35	2.69±.01	.17±.01	6.32±.51
448-5	F_3	1917	2.7	309	2.88±.01	.19±.01	6.60±.18
448-5 (4 plants)	F_4	1918	2.7 to 3.0	35	2.86±.05	.45±.04	15.73±1.29
448-7	F_3	1917	2.8	39	2.74±.03	.28±.02	10.22±.78
448-7-1	F_4	1918	3.0	107	2.21±.01	.17±.01	7.69±.35
448-7-3	F_4	1918	2.1	102	3.12±.01	.18±.01	5.77±.27
448-7-4	F_4	1918	3.2	113	2.96±.02	.32±.01	10.81±.49
448-8	F_3	1917	2.8	69	2.88±.04	.52±.03	18.06±1.07
448-9	F_3	1917	3.0	49	2.85±.06	.61±.04	21.40±1.52
448-9-4	F_4	1918	2.3	63	2.06±.01	.14±.01	6.80±.41
448-9-7	F_4	1918	2.5	142	2.64±.03	.53±.01	20.08±.84
448-9-14	F_4	1918	3.0	44	2.57±.03	.27±.02	10.51±.76
448-9-16	F_4	1918	3.2	104	3.34±.03	.65±.03	19.46±.94
448-9-19	F_4	1918	4.4	16	3.41±.04	.25±.03	7.33±.87
448-9-29	F_4	1918	4.5	128	3.52±.04	.62±.03	17.61±.94
448-9-30	F_4	1918	3.0	59	4.30±.01	.20±.01	4.65±.29
448-10	F_3	1917	3.4	58	2.96±.04	.41±.03	13.85±.87
448-11	F_4	1918	3.0	73	3.36±.02	.23±.01	6.83±.43
448-11-2	F_4	1918	3.5	45	3.08±.01	.17±.01	5.52±.31
448-11-3	F_4	1918	3.5	84	3.69±.02	.16±.01	4.34±.31
448-11-4	F_3	1917	3.5	55	3.45±.02	.25±.01	7.25±.38
448-12	F_4	1918	3.1	53	3.51±.05	.60±.04	17.09±1.12
448-13	F_3	1917	4.2	126	3.57±.04	.43±.08	12.04±.80
448-13-1	F_4	1918	2.8	64	3.84±.03	.46±.02	11.98±.51
448-13-2	F_4	1918	2.8	57	3.19±.02	.20±.01	6.27±.37
448-13-5	F_4	1918	4.3	65	4.15±.03	.19±.01	4.58±.29
448-14	F_3	1917		55	2.52±.03	.39±.01	15.48±.93
448-15	F_3	1917		40	3.91±.02	.38±.02	9.72±.63
448-16	F_3	1917		331	4.37±.01	.22±.01	5.03±.38
448-16 (4 plants)	F_4	1918	4.3 to 4.8	51	4.30±.03	.27±.01	6.28±.16
448-17	F_3	1917	3.6	38	3.67±.04	.40±.03	10.90±.74
448-18	F_3	1918	4.0	30	4.02±.05	.45±.03	11.19±.87
448-19	F_3	1917	3.9	30	3.67±.06	.46±.04	12.53±1.10
448-20	F_3	1917	4.1	40	4.19±.03	.34±.03	8.11±.61

The Svanhals parent gave a mean of 2.71 ± 0.01 mm. and the Manchuria one of 3.46 ± 0.01 mm. in 1918. No sorts were obtained which were homozygous for densities very different from those of the parents.

FAMILY MANCHURIA (360) × STEIGUM (17).

The parental forms of the Manchuria and Steigum cross gave nearly the same average density in 1916. In 1918 the Manchuria parent gave about the same average density as in 1916, but the Steigum averaged somewhat higher than in the previous year. The coefficient of variability of the Manchuria parent in 1917 was 4.19 ± 0.15 mm.; of the Steigum parent, 4.90 ± 0.17 mm.; and of the F_2 generation which was grown in 1916, 7.69 ± 0.21 mm. The data are reported in Table II (sec. B).

As Table II shows, some forms bred true in F_3 and in F_4, while others were as variable as the F_2 generation. Selection 368–22 in the F_3 and F_4 generations gave means of 3.21 ± 0.02 and 3.29 ± 0.01 mm., respectively. When compared with the parental forms, it seems that we have here a lower density line than either parent. As the number of individuals is small in many F_3 lines, it does not seem profitable to analyze more closely the results obtained.

FAMILY PYRAMIDATUM (476) × JET (454).

Table II (sec. C) shows that the parental forms of the cross between Pyramidatum and Jet are of very different densities. The Pyramidatum parent gave a mean density of 2.11 ± 0.01 mm. in 1918; the Jet, 3.92 ± 0.01 mm.; while the F_1 generation averaged 2.86 ± 0.01 mm. The F_1 generation is, therefore, slightly more dense than the parental average, which is 3.01 mm. This is quite different from the F_1 generation in the cross between Manchuria and Svanhals, in which there was an almost complete dominance of the dense over the lax form.

The F_2 generations were grown both in 1916 and in 1918. The means for these two F_2 generations were about the same as the parental average, being 2.92 ± 0.04 mm. and 3.10 ± 0.03 mm., respectively. The highest coefficient of variability for the Jet parent is 6.93 ± 0.39 mm., while the highest coefficient for Pyramidatum is 6.16 ± 0.21 mm. The coefficients of variability for the two F_2 generations are 16.44 ± 0.87 mm. and 18.38 ± 0.81 mm., respectively, while the frequencies of the F_2 generations range from above the modal class of the lax parent to the modal class of the dense parent. It is of interest to note that with a total of 87 F_1 plants, none were of the same frequency range as that of the parents, all being of intermediate density. Of the 22 F_2 plants continued in F_3, ten would have been included within the limits of this F_1 population. Of these ten, eight gave about as variable a progeny as the F_2 generation, while two

appeared to give homozygous dense progeny. Of the entire 22 plants, representing all types of F_2 densities, nine proved about as variable in F_3 as the F_2 generation.

Seven F_3 selections which appeared to be breeding true, as determined by the frequency distribution and coefficient of variability, were tested in the F_4 generation. This was done by selecting 10 heads of different densities and growing the progeny of each separately. Where all heads gave similar results, they are combined in the table and are given as the result of 10 plants.

The F_3 line 325–5, of which only 26 plants were available for study, gave a mean of 3.15 ± 0.02 mm. in 1917, with a low coefficient of variability. On testing this line in 1918, when data from 213 plants were available, a somewhat higher mean was obtained, or 3.43 ± 0.01 mm. Its coefficient of variability is also somewhat larger than in the homozygous parental forms. Selection 325–15 proved pure in F_4 with the exception of the progeny of one plant which gave as great a variability as the F_2 generation. Why one plant should behave so differently from the nine others is difficult to explain. The possibility of a natural cross must not be overlooked, although observations show that these are very infrequent. An occasional error is also a possibility, although precautions were taken to eliminate these as far as possible.

The F_4 means for the seven lines which gave evidence in F_3 and F_4 indicating that they were homozygous are as follows: 325–5 (10 plants), 3.43 ± 0.01 mm.; 325–13 (10 plants), 3.47 ± 0.01 mm.; 325–16 (9 plants), 3.74 ± 0.01 mm.; 325–18 (10 plants), 2.24 ± 0.01 mm.; 325–20 (10 plants), 2.47 ± 0.02 mm.; 325–21 (10 plants), 3.95 ± 0.01 mm.; 325–22 (10 plants), 3.72 ± 0.01 mm.

Of these, five have mean densities which are not very different from that of the Jet (lax) parent, while the means of the other two are similar to that of the Pyramidatum parent. The most dense and the least dense of the five lax homozygous segregates have mean internode lengths of 3.43 ± 0.01 mm. and 3.95 ± 0.01 mm., respectively. As great a difference as this in any one season would not be expected in a sort homozygous for similar characters. It is not much greater, however, than seasonal variation in the means of several of the pure 2-rowed forms, which seem more susceptible to such variability than the 6-rowed parents. Inheritance of such a reaction difference might possibly explain the results here represented. Whatever explanation may be given for these new means, here, as in the Manchuria × Svanhals cross, no homozygous forms were produced which differed materially in density from the density of one or the other parent.

FAMILY HANNA (460) × REID TRIUMPH (404).

The parental forms, Hanna and Reid Triumph, are of distinctly different densities, and there is no overlapping of frequency distributions during the three years in which they have been grown. In Table II (sec. D) the mean of the Hanna parent ranges from 4.12 ± 0.02 mm. in 1916 to 4.56 ± 0.01 mm. in 1918. The Reid Triumph variety has much less seasonal variation, the mean in 1917 being 2.73 ± 0.01 mm. and in 1916, 2.64 ± 0.01 mm. It is of interest to note that the Reid Triumph has about the same average mean as the Svanhals 2-rowed form, while the Hanna is considerably more lax than the Manchuria form which was crossed with the Svanhals variety.

The F_2 generation of the cross between Hanna and Reid Triumph proved more variable than the parents and frequently gave distribution from below the mode of the Reid Triumph to considerably above the mode of the Hanna parent. Twenty F_2 plants were grown in F_3, some giving as variable a population as obtained in F_2, while other F_3 lines were no more variable than the parental forms.

Fourteen of these F_3 lines which gave the clearest indication of being homozygous were further tested in the F_4 generation. The method was similar to that previously used, 4 to 10 plants of a line being grown and the combined result being the basis of conclusions as to purity. Of the 14 lines tested in F_4, 8 gave evidence in the combined F_3 and F_4 data to show that they are homozygous for density.

Those which are of questionable purity will be briefly considered. Selection 406–3 gave a mean of about the same density as the Reid Triumph parent, but the coefficient of variability is somewhat higher than in the pure parental lines. Selection 406–4 proved to be heterozygous. One of the head selections, 406–4–3, produced a type which seems pure for density. The mean of this line is 3.72 ± 0.03 mm. Selection 406–9 seems to be heterozygous. Probably 406–9–1 is homozygous, the average mean being about the same as that of the Hanna parent. Selection 406–10 also is more variable than the pure parental variety. The frequency distribution indicates that fewer density factors are involved than in the F_2 generation. Selections 406–16 and 406–18 appear to be heterozygous. In later generations two selections of 406–18 seem to be homozygous. Thus 406–18–5 is probably breeding true with a mean density of 3.40 ± 0.02 mm., while 406–18–9 gives evidence of being homozygous for a mean of 2.66 ± 0.02 mm.

Those which seem nearly homozygous by an examination of their frequency ranges and coefficients of variability as obtained in F_3 and F_4 generations are as follows: 406–1, mean 2.81 ± 0.01 mm.; 406–5, mean 4.43 ± 0.01 mm.; 406–7, mean 2.43 ± 0.01 mm.; 406–8, mean 4.32 ± 0.01 mm.; 406–11, mean 4.32 ± 0.02 mm.; 406–12, mean,

2.84±0.02 mm.; 406–19, mean 3.29±0.01 mm.; 406–22, mean 4.37±0.01 mm.

Aside from these, individual heads grown in F_4 which appear to give homozygous progeny as a result of the single season's test are as follows: 406–4–3, mean 3.72±0.03 mm.; 406–9–1, mean 4.30±0.04 mm.; 406–18–5, mean 3.40±0.02 mm.; 406–18–9, mean 2.66±0.02 mm.

The means for these four F_4 families are somewhat unreliable because of the small number of individuals grown. All coefficients of variability, however, are very small.

These results show that homozygous intermediates may be produced, as well as homozygous types, which give about the same average density as the parental forms. No analysis of average differences as small as 0.2 to 0.3 mm. has been attempted. The fact that environmental or other seasonal characters may modify the expression of a character nullifies such close analysis.

FAMILY HANNA (460) × ZEOCRITON (1039).

The Hanna used in the cross with Zeocriton is the same pure line that was used in the cross with Reid Triumph. Zeocriton is a very dense 2-rowed form. This cross is between the most dense and the most lax form used in this study.

The F_2 generation shown in Table II (sec. E) ranged from above the modal class of Hanna to the modal class of Zeocriton, even though only 141 individuals were studied. It has a correspondingly high coefficient of variability.

An examination of the coefficients obtained in later generations show that some are as large as those obtained in the F_2 line. Others are intermediate, being significantly larger than any obtained in the pure forms, while still others are as small as those obtained for the pure parental lines. This would indicate that the mode of inheritance was more complex than in the cross between Pyramidatum × Jet previously mentioned.

Selection 448–9, which was almost as variable in the F_3 as in the F_2 generation, was selected for further experiment, the progeny of 30 plants being measured in the F_4 generation. Data from 7 of the 30 progeny lines are presented, as the remaining 23 all appeared to be segregating. Results of density studies in F_4 lines 448–9–7, 448–9–14, 448–9–16, and 448–9–29 are given, as these indicate the segregation obtained in the unpresented lines. No F_4 line of greater coefficient of variability than 448–9–7 was obtained, and none with a wider frequency range than 448–9–16. Three lines appear to be homozygous, as determined by the frequency distribution and coefficient of variability. These are shown in Table III.

TABLE III.—*Homozygous plants of selection 448–9 of the Hanna-Zeocriton cross, F_4 generation.*

F_4 line.	Number of individuals.	Mean.	Coefficient of variability.
		Millimeters.	
448–9–4	63	2.06±0.01	6.80±0.41
448–9–19	16	3.41± .04	7.33± .87
448–9–30	59	4.30± .02	4.65± .29

The mean of 448–9–19 is not as reliable as of the other two lines, as only 16 individuals were available for the study.

Selections 448–7 and 448–13 appear heterozygous in the F_3 generation and have about the same degree of frequency range. The coefficients of variability are much smaller than in F_2, but are significantly larger than in the pure parental forms. The frequency range for 448–7, of which 39 plants were studied, was from 2.0 to 3.2 mm. Two plants from each of these lines gave evidence of being homozygous in F_4. These are shown in Table IV.

TABLE IV.—*Homozygous plants of selections 448–7 and 448–13 of the Hanna-Zeocriton cross, F_4 generation.*

F_4 line.	Number of individuals.	Mean.	Coefficient of variability.
		Millimeters.	
448–7–1	107	2.21±0.01	7.69±0.35
448–7–3	102	3.12± .01	5.77± .27
448–13–2	64	3.19± .02	6.27± .37
448–13–5	57	4.15± .02	4.58± .29

Four of the 20 F_2 plants which were tested in F_3 appeared to give homozygous progeny. Three of these proved to be homozygous by further test, while one, 448–11, proved heterozygous. The F_4 lines of interest which seem to be homozygous are shown in Table V.

TABLE V.—*Homozygous plants of selection 448–11 of the Hanna–Zeocriton cross, F_4 generation.*

F_4 line.	Number of individuals.	Mean.	Coefficient of variability.
		Millimeters.	
448–11–2	73	3.08±0.01	5.52±0.31
448–11–3	45	3.69± .02	4.34± .31

The three lines of especial interest which appeared homozygous by both the F_3 and F_4 study are as follows: 448–1, mean 2.30 ± .01 mm.; 448–5, mean 2.88 ± .01 mm.; 448–16, mean 4.30 ± .01 mm. The F_4 generation means are given for these lines, as they are based upon larger numbers than the F_3 test. Typical spikes of the parent varieties and of these lines are shown in Plate II.

In the Hanna × Zeocriton cross there are a number of homozygotes of a density intermediate between the densities of the parents. The homozygotes of this cross appear to fall in groups. Three near the dense parent have internode lengths ranging from 2.06 to 2.30 mm. Three near the lax parent have internode lengths ranging from 4.15 to 4.30 mm. Four moderately dense intermediates have internode lengths varying from 2.88 to 3.19 mm., and two lax intermediates have internode lengths of 3.41 and 3.69 mm. This grouping is arbitrary, as the difference between the two intermediate groups is little more than between individuals of either intermediate group. Some homozygous intermediates from this cross have densities approximately the same as those of parents used in other crosses studied.

SUMMARY OF RESULTS.

The observational accuracy is such that differences in density greater than 0.2 mm. are significant when the measurements are taken in the middle part of the spike.

Except in the Hanna and Steigum varieties the seasonal fluctuations in the means of the parents were not more than 0.2 mm. The seasonal variations in the means of the 2-rowed were greater than in the 6-rowed varieties.

The density of the F_1 generation does not have an unvarying relation to the density of the parents. In the Svanhals × Manchuria cross density is dominant in the F_1 generation. In the Pyramidatum × Jet cross it was intermediate.

The two F_1 generations grown were no more variable than the parental sorts and all crosses gave segregation in F_2. Although the number of F_2 plants grown averaged no greater than that of the parental forms, the frequency ranges extended from the modal class of one parent to the modal class of the other and often beyond these classes.

The F_3 generation contained progeny groups which were no more variable for length of rachis internode than pure lines of the parents. Rather extensive studies of a number of F_4 generations gave further evidence of purity of several of these F_3 lines.

The Manchuria × Svanhals and Pyramidum × Jet crosses gave forms homozygous for densities similar to those of the parents but none homozygous for intermediate densities. Crosses between Hanna and Reid Triumph and between Hanna and Zeocriton gave types homozygous for densities intermediate between the densities of the parents, as well as near those of their parents. The latter cross produced homozygous forms similar to Reid Triumph, Hanna, and their homozygous intermediates, as well as forms like the Zeocriton parent. The range of means of these homozygous forms was almost continuous, although there was an indication of two centers of intermediate

density. More extensive study would be needed to determine whether these apparent centers are of any significance.

DISCUSSION OF RESULTS.

From the fact that segregates homozygous for density are apparent in the measurements of the F_3 and F_4 generations, it seems safe to conclude that internode length in the barley rachis may be explained on the factor hypothesis. The number or value of the factors involved is not readily estimated. In a general way the results of the Manchuria × Svanhals and the Pyramidatum × Jet crosses seem to indicate a single main factor difference. The proportion of homozygotes is roughly satisfactory, and the absence of homozygotes differing greatly from the mean of their parents is also in favor of this belief. The dominance of density in the F_1 generation in the first cross and its intermediate expression in the second is of interest.

The results in the Hanna × Reid Triumph cross in the same way indicate a broad difference of two factors. In this cross forms were isolated that were homozygous for intermediate densities, as well as forms having densities near those of the parents. These results can be interpreted very satisfactorily on the basis of two main factors for internode length. These factors are cumulative in effect, both being necessary to produce the extreme type. The results show that a sort may be homozygous for one of the factors and heterozygous for the other. At least, heterozygous forms whose progeny range is from the intermediate group to one or the other parent are so interpreted.

The Hanna × Zeocriton cross gave homozygous intermediates of unlike value, as well as homozygous sorts which were like the parents. If the presence and absence hypothesis is here used, three main factors may be postulated to explain the genetic facts. These factors may be supposed to be of like value, each inherited independently, each allelomorphic to its absence, the number showing a heterozygous condition being half the homozygous sorts. This hypothesis explains the genetic fact fairly well. Other minor factor differences are doubtless necessary to explain all of the results. One known minor character of some density significance separates the parental forms. This is a difference in the progressive density from the base to the tip of the rachis, the Zeocriton parent being the only sort which shows a constant increase in length of internode from the base to the tip of the spike.

A comparison of the Pyramidatum × Jet cross with the Hanna × Zeocriton cross illustrates some facts regarding the mode of inheritance of density. These are the two widest crosses made in the study. The first produced no homozygous intermediates. The second produced many. An F_1 generation was grown of the Pyramidatum ×

Jet cross. It was of intermediate density and no more variable than the parental forms. The second generation is shown in figure 1 as a multimodal curve with peaks at densities corresponding to those of the parents and the F_1 generation. The homozygous forms produced closely approximated the densities of the parental varieties, as is illustrated by the curves. Although there is considerable variability in the means of the more lax segregates, this is no greater than the seasonal variation of the means of several of the 2-rowed forms.

The contrast between the Pyramidatum × Jet and the Hanna × Zeocriton crosses is very striking. Each showed wide segregation
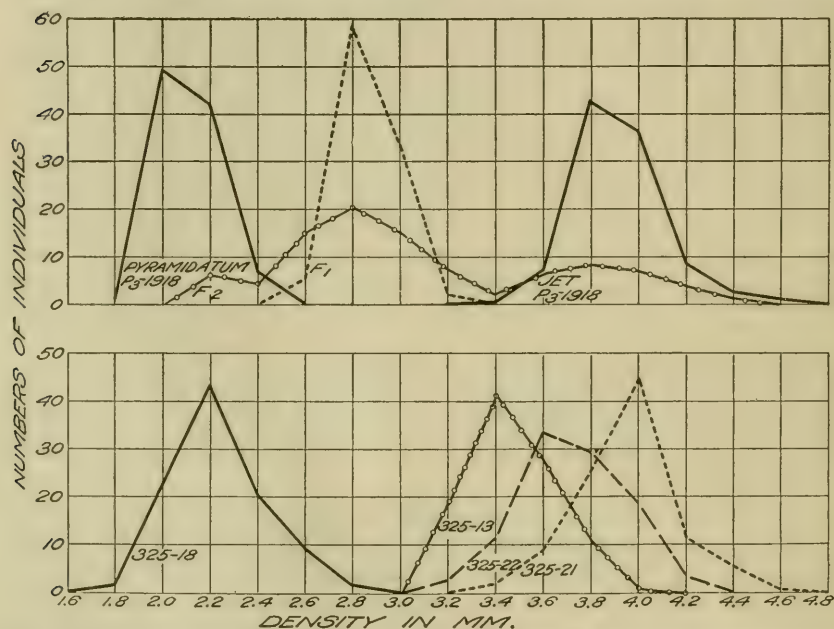

FIG. 1.—Diagrams showing the densities of parental forms and F_1 and F_2 generations of a cross between the Pyramidatum and Jet barleys (upper) and of four homozygous forms from this cross in the F_3 generation (lower).

in the F_2 generation. Hanna × Zeocriton, however, produced a much smaller proportion of homozygous forms in F_3 and F_4 than the Pyramidatum-Jet cross. Homozygous intermediates as well as forms with the parental densities were produced in the F_3 generation. The heterozygous lines were of different types, some being as variable as the F_2, while others were more variable than the pure forms, but less so than the F_2 generation. The means of the heterozygous forms were also of different values. The results are illustrated in figure 2. These graphs show the parental and F_2 types and four pure F_3 forms of unlike densities, as well as the heterozygous lines obtained. This cross has given nearly all sorts of densities, and by this one cross the different densities of the parental forms used in these experiments have been again obtained.

These results show that, although density is a very stable size character, in some crosses numerous factors are involved which, by recombination, produce homozygous forms showing an almost continuous range of density from the very lax to the dense types. It is only reasonable to conclude that if a greater number of varieties had been studied, together with crosses between them, a continuous range for the average length of internode of homozygous forms could be obtained which would show only small differences in average density between types. These results are of considerable interest in barley classification. While dependable in the isolation and description of
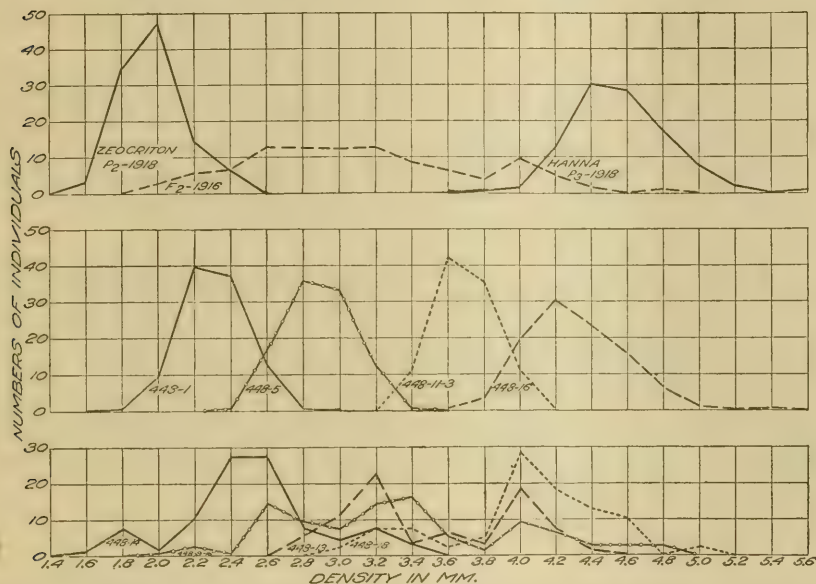

Fig. 2.—Diagrams showing the densities of parental forms and of the F_2 generation in a cross between the Zeocriton and Hanna barleys (upper), of four pure lines (middle), and of several heterozygous lines (lower).

strains, groups founded on this character are likely to overlap and hence to be of limited value for taxonomic purposes.

While the general genetic results of these crosses are explained on a broad factor basis of differences of one to three factors, the fact remains that the homozygous segregates corresponding to the parents do not always have the exact density of the parents. Likewise, the forms homozygous for intermediate densities do not all fall together but in groups, which, in the Hanna $\times$ Zeocriton cross become almost continuous, even where limited numbers are concerned, and might become wholly continuous if it were possible to carry the full number to the fourth generation. Obviously, there are modifying factors, and so far as they affect density they may be considered as minor density factors. Several explanations are possible. These varia-

tions may be associated with the same variability which manifests itself in seasonal fluctuations. They may be due to the differences in the progressive density from the base to the tip of the rachis, which is more marked in some than in other varieties. Other explanations might be suggested, but in the absence of definite proof it seems unwise to attempt a more detailed analysis of the results.

CONCLUSIONS.

Despite the handicaps of the investigations, a number of points are established.

(1) Internode length in the barley rachis is a very stable character, which is much less affected by environmental conditions than many size characters.

(2) Segregation occurs in the F_2 generation of crosses, and forms homozygous for density appear in this generation, their purity being demonstrated in the F_3 generation.

(3) In some crosses new lines with densities differing much from those of their parents can not be secured, while in others lines with very different densities may be isolated.

(4) The inheritance of internode lengths may be interpreted on the factor hypothesis. Some of the crosses studied appeared to differ by a single main factor of density, while in others two or three main factors are necessary to explain the genetic results. Minor factors were evident whose number or nature was not established and through whose action the means of homozygous forms of intermediate densities in some crosses may become more or less continuous between the means of the parents.
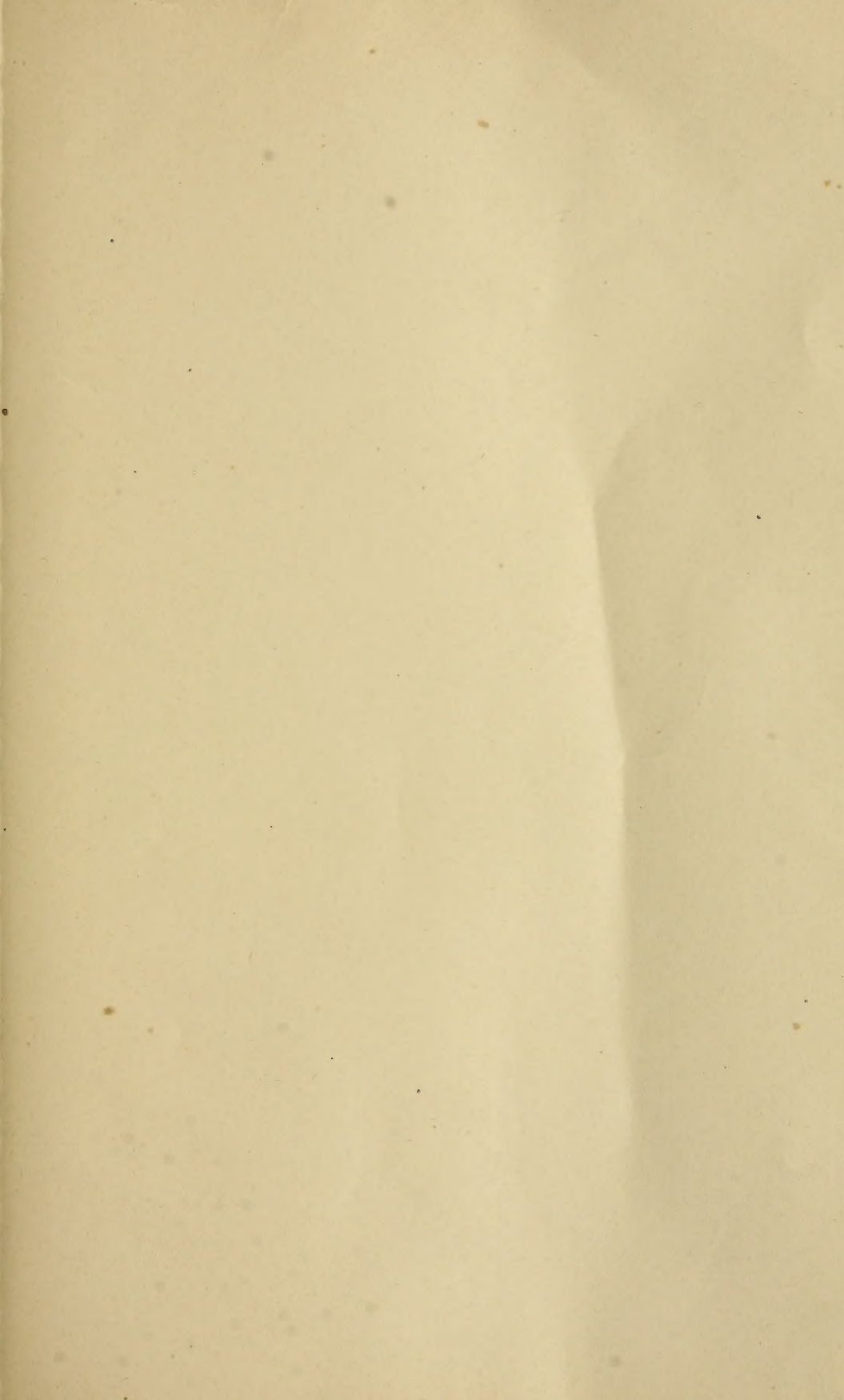
LITERATURE CITED.

(1) ALEFELD, F. G. C.
    1866. Landwirtschaftliche Flora . . . 363 p. Berlin.

    ATTERBERG, ALBERT.

(2)   1889. Die Erkennung der Haupt-Varietaten der Gerste in den nordeuro-
        päischen Saat-und Malzgersten. *In* Landw. Vers. Stat., Bd. 36, p. 23–27.

(3)   1891. Die Klassification der Saatgersten Nord-Europas. *In* Landw. Vers.
        Stat., Bd. 39, p. 77–80.

(4)   1899. Die Varietaten und Formen der Gerste. *In* Jour. Landw., Bd. 47,
        Heft 1, p. 1–44.

(5) BEAVEN, E. S.
    1902. Varieties of barley. *In* Jour. Fed. Inst. Brewing, v. 8, no. 5, p. 542–
        593, 12 fig. Discussion, p. 594–600.

(6) BIFFEN, R. H.
    1907. The hybridization of barleys. *In* Jour. Agr. Sci., v. 2, pt. 2, p.
        183–206.

(7) BLARINGHEM, L.
    1910. Etudes sur l'amélioration des crus d'orges de brasserie. 288 p., illus.

(8) ERIKSSON, JACOB.
    1889. Collectio cerealis. Varietates cerealium in Suecia maturescentes
        continens, fasc. 1, 10 p., 2 fig. Stockholm.

    HARLAN, H. V.

(9)   1914. Some distinctions in our cultivated barleys with reference to their
        use in plant breeding. U. S. Dept. Agr. Bul. 137, 38 p., 16 fig.
        Literature cited, p. 37–38.

(10)   1918. The identification of varieties of barley. U. S. Dept. Agr. Bul. 622,
        32 p., 4 pl. Literature cited, p. 31–32.

    HEUZÉ, GUSTAVE.

(11)   [1872.] Les plantes alimentaires. 2 v., illus. Paris.

(12)   1896–97. Les plantes céréales. Ed. 2, 2 v., illus. Paris.

    KOERNICKE, F. A.

(13)   1873. Systematische Uebersicht der Cerealien und monocarpischen Legumi-
        nosen . . . 55 p., 1 tab. Bonn.

(14)   1882. Die Saatgerste. Hordeum vulgare 1. sensu latiere. *In* Ztschr.
        Gesam. Brauw., Jahrg. 5, p. 113–138, 161–172, 177–186, 193–203, 205–
        208, 304–311, 329–336, 393–413. Pl. 5–14.

(15)   1885. Handbuch der Getreidebaues. 2 Bd. Berlin.

(16)   1895. Die hauptsächlichsten Formen der Saatgerste . . . 15 p. Bonn.

(17)   1908. Die Entstehung und das Verhalten neuer Getreidevarietäten. *In*
        Arch. Biontol., Bd. 2, Heft 2, p. 389–437.

(18) LINNÉ [LINNÆUS], CARL VON.
    1753. Species plantarum . . . t. 1. Holmiae.

(19) NEWMAN, L. H.
    1912. Plant breeding in Scandinavia. 193 p., 63 fig. Ottawa. Literature
        cited, p. 188–193.

(20) NILSSON-EHLE, H.
    1909. Kreuzungsuntersuchungen an Hafer und Weizen. 122 p. Lund.

(21) PARKER, W. H.
    1914. Lax and dense eared wheats. *In* Jour. Agr. Sci., v. 6, no. 3, p. 371–386,
       fig. 1, pl. 1.

(22) SCHUEBLER, GUSTAV.
    [1818.] Dissertatio inauguralis botanica sistens characteristicen et descrip-
       tiones cerealium in horto academico Tubingensi et in Würtem-
       bergia . . . 47 p., pl. Tubingae. Inaug. Diss.

(23) SERINGE, N. C.
    1841–42. Descriptiones et figures des céréales Européennes. *In* Ann. Soc.
       Roy. Agr. Lyon, t. 4, p. 321–384, pl. 1–9, 1841; t. 5, p. 103–196, pl.
       2–10, 1842.

(24) TSCHERMAK, ERICH VON.
    1914. Die Verwertung der Bastardierung für phylogenetische Fragen in der
       Getreidegruppe. *In* Ztschr. Pflanzenzücht., Bd. 2, Heft 3, p.
       291–312.

(25) VOSS, A.
    1885. Versuch einer neuen Systematik der Saatgerste. *In* Jour. Landw.,
       Jahrg. 33, Heft 3, p. 271–282.